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LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *NEASPILOTA FOOTEI* FREIDBERG AND MATHIS (DIPTERA: TEPHRITIDAE) ON *ASTER OCCIDENTALIS* (NUTTALL) TORREY AND A. GRAY (ASTERACEAE) IN SOUTHERN CALIFORNIA

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Abstract.—*Neaspilota footei* Freidberg and Mathis is a univoltine, monophagous or nearly monophagous, fruit fly (Diptera: Tephritidae) developing in the flower heads of *Aster occidentalis* (Nuttall) Torrey and A. Gray (Asteraceae) belonging to the subtribe Asterinae of the tribe Astereae in southern California. It also has been reported from *Conyza* (as *Erigeron*) *canadensis* (L.) (Cronquist) (and as *E. pusillus*) and *Chrysothamnus* sp., but both of these host records need confirmation. The egg, first-, second- and third-instar larvae and puparium are described and figured, and these immature stages are compared with those of other *Neaspilota.* The anterior thoracic spiracles of the second and third instars of *N. footei* have three papillae. The second and third instars also have an undetermined number of oral ridges with dentate posterior margins in a vertical series lateral to the oral cavity. The appearance and placement of these oral ridges is a distinguishing generic larval character. The larvae feed mainly on the corollas of florets and ovules as first instars; on corollas, ovules, and soft achenes as second instars; but as third instars, they feed mainly on ovules and soft achenes. A single annual generation is produced on *A. occidentalis* in southern California. The life cycle is of the aggregative type and overwintering mainly occurs as puparia attached to uneaten achenes and fragments thereof in dead flower heads. *Pteromalus* sp. (Hymenoptera: Pteromalidae) was reared as a solitary, larval-pupal endoparasitoid of *N. footei*; *Eurytoma* sp. (Hymenoptera: Eurytomidae) and *Mesopolobus* sp., as probable, solitary, larval-pupal endoparasitoids.

Key Words: Insecta, *Neaspilota, Aster,* Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, allopatry, flower-head feeding, aggregative life cycle, seed predation, parasitoids

Revision of the genus *Neaspilota* (Diptera: Tephritidae) by Freidberg and Mathis (1986) facilitated identification of specimens reared from California Asteraceae (Goeden 1989) and stimulated several life-history studies, including those on *N. viridescens* Quisenberry (Goeden and Headrick 1992), *N. wilsoni* Blanc and Foote (Goeden and Headrick 1999), *N. signifera* (Coquillett) (Goeden 2000a), *N. aenigma* Freidberg and Mathis (Goeden 2000b), *N. appendiculata* Freidberg and Mathis (Goeden 2000c), *N. pubescens* Freidberg and Mathis (Goeden 2000d), and *N. achilleae* Johnson (Goeden 2001). This paper describes the immature stages and life history of an eighth species from California, *N. footei* Freidberg and Mathis, and is the last paper in this series on *Neaspilota.*

MATERIALS AND METHODS

The present study was based in large part on dissections of samples of flower heads of *Aster occidentalis* (Nuttall) Torrey and A. Gray (Asteraceae) mainly collected on the north shore of Big Bear Lake at 2,020-m elevation, Serrano Meadows Picnic Area, San Bernardino Nat. Forest (N Section), SW San Bernardino Co., during 1996 and 1997. One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Three eggs, six first-, 14 second-, and 15 third-instar larvae and seven puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional prepuparia and puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied and photographed with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated prepuparia and puparia were individually caged in 850-ml clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for studies of longevity and sexual maturation in the insectary of the Department of Entomology, University of California, Riverside, at 25 ± 1°C, and 14/10 (L/D) photoperiod. A single pair of a virgin male and female obtained from emergence cages also were held in a clear-plastic, petri dish provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden (2000a, b, c, d, 2001), Goeden et al. (1998), Goeden and Headrick (1992, 1999), Goeden and Teerink (1997a, b, 1998, 1999a, b), Teerink and Goeden (1999), and our earlier works cited therein. Means ± SE are used throughout this paper. Voucher specimens of *N. footei* immature stages, adults, and parasitoids reside in my research collections.

RESULTS AND DISCUSSION

TAXONOMY

Adult.—*Neaspilota footei* was described by Freidberg and Mathis (1986, p. 49–52), who pictured the unpatterned wing, along with drawings (p. 50) of the lateral aspect of the head, male right foretarsus, epandrium, distiphallus, epandrium and cerci, aculeus and its apex enlarged, and spermatheca.

Immature stages.—The egg, first-, second- and third-instar larvae, and puparium are described below for the first time.

Egg: Fifty-four eggs dissected from field-collected flower heads were white, opaque, smooth, elongate-ellipsoidal, 0.62 ± 0.004 (range, 0.56–0.68) mm long, 0.17 ± 0.002 (range, 0.16–0.20) mm wide, smoothly rounded at tapered basal end (Fig. 1A); pedicel button-like, 0.02 mm long, circumscribed apically by semicircular or elliptical aeropyles arranged singly or in two compressed or separate rows parallel to the long axis of the egg (Figs. 1B, C).

The egg of *N. footei* is similar in shape

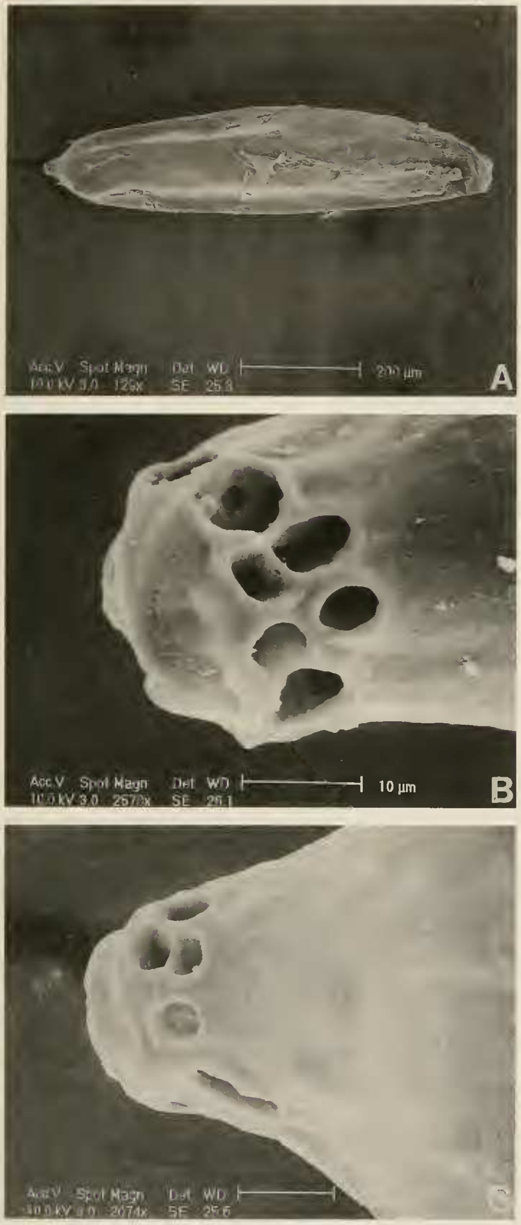

Fig. 1. Egg of *Neaspilota footei:* (A) habitus, anterior end to left; (B) pedicel showing pattern of aeropyles; (C) pedicel of a different egg with its aeropyles.

to those of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), and *N. appendiculata* (Goeden 2000c). The egg of *N. footei* is about 10% longer on average than the eggs of *N. viridescens* (Goeden and Headrick 1992), but about 30% shorter and narrower than those of *N. wilsoni* (Goeden and Headrick 1999) and about 10% shorter than those of *N. appendiculata* (Goeden 2000c); the latter two species have the largest adults among southern California *Neaspilota* (Freidberg and Mathis 1986). The aeropyles of *N. appendiculata* are arranged in one to three rows around the apex of the pedicel (Goeden 2000c), those of *N. viridescens* are irregularly scattered around the apex (Goeden and Headrick 1992), and those of *N. wilsoni* fully cover the pedicel (Goeden and Headrick 1999).

First instar: White, elongate-cylindrical, bluntly rounded anteriorly and posteriorly (Fig. 2A); body segments well-defined, nearly free of minute acanthae; gnathocephalon smooth, lacking oral ridges, with pair of prominent integumental petals dorsad of mouthhooks (Figs. 2B-1, C-5); dorsal sensory organ a well-defined, dome-shaped papilla (Figs. 2B-2, C-1, D-1); anterior sensory lobe (Figs. 2B-3, C-2, D-2) bears terminal sensory organ (Figs. 2C-3, D-3); lateral sensory organ (Fig. 2D-4), supralateral sensory organ (Fig. 2D-5), and pit sensory organ (Fig. 2D-6); stomal sense organ ventrolaterad of anterior sensory lobe (Figs. 2B-4, C-4, D-7), integumental petal (Figs. 2B-1, C-5, D-8) fused laterally with stomal sense organ (Figs. 2B-4, C-4, D-7); mouthhook bidentate (Figs. 2B-5, C-6); median oral lobe laterally flattened (Figs. 2B-6, C-7), posterolateral pair of verruciform sensilla on gnathocephalon (Figs. 2B-7, C-8); meso- and metathoracic and abdominal lateral spiracular complexes not seen; caudal segment with two stelex sensilla, dorso- and ventrolaterad of posterior spiracular plate (Fig. 2E-1), neither stelex sensillum basally ringed with minute acanthae; posterior spiracular plate bears two ovoid rimae, ca. 0.004 mm in length (Fig. 2E-2), and four interspiracular processes, each with two to four branches, longest measuring ca. 0.01 mm (Fig. 2E-3); intermediate sensory complex with one stelex

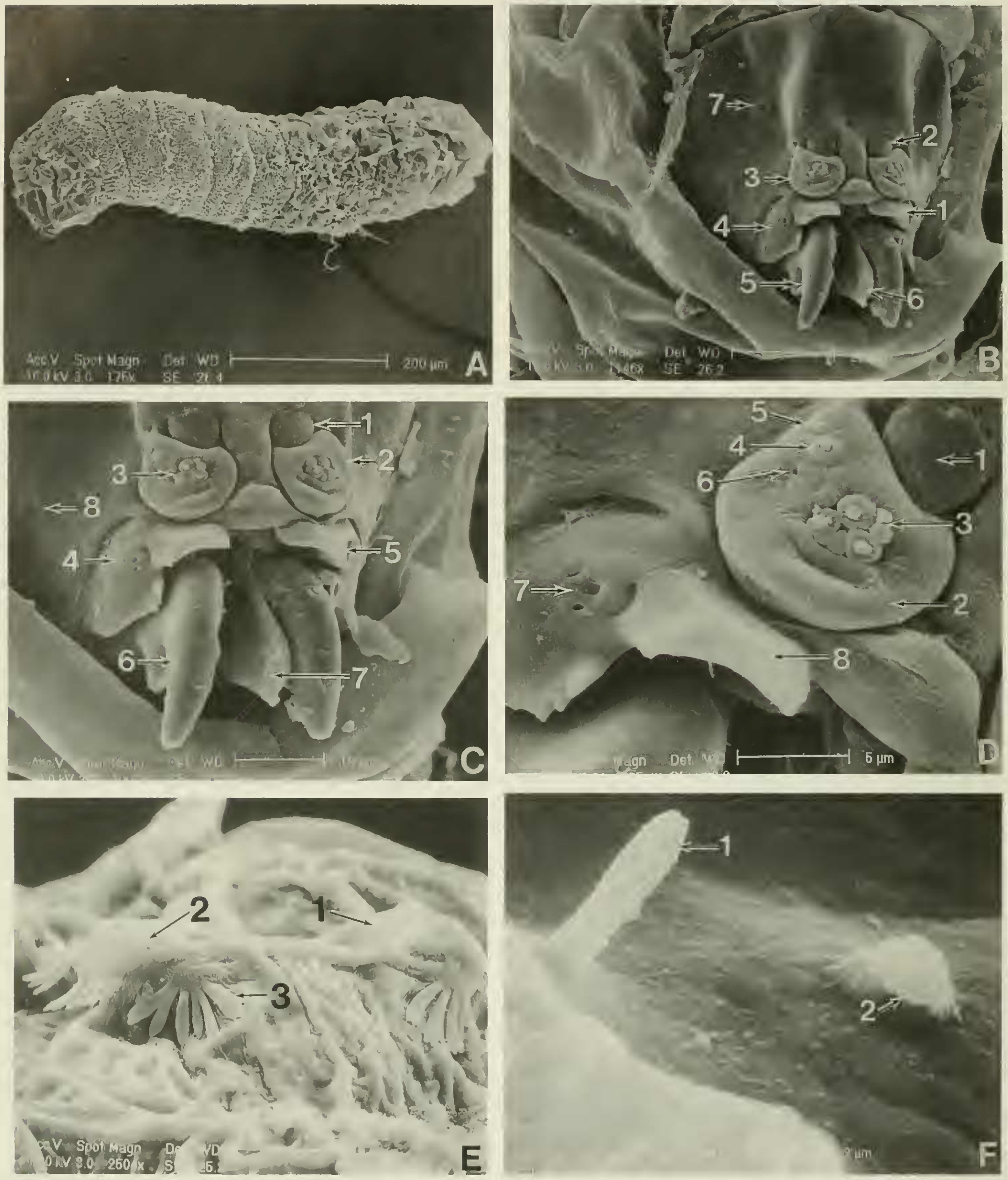

Fig. 2. First instar of *Neaspilota footei:* (A) habitus, anterior to left; (B) gnathocephalon, frontolateral view, 1 — integumental petal, 2 — dorsal sensory organ, 3 — anterior sensory lobe, 4 — stomal sense organ, 5 — mouthhook, 6 — median oral lobe, 7 — verruciform sensillum; (C) 1 — dorsal sensory organ, 2 — anterior sensory lobe, 3 — terminal sensory organ, 4 — stomal sense organ, 5 — integumental petal, 6 — mouthhook, 7 — median oral lobe, 8 — verruciform sensillum; (D) 1 — dorsal sensory organ, 2 — anterior sensory lobe, 3 — terminal sensory organ, 4 — lateral sensory organ, 5 — supralateral sensory organ, 6 — pit sensory organ, 7 — stomal sensory organ, 8 — integumental petal; (E) caudal segment, 1 — posterior spiracular plate, 2 — rima, 3 — interspiracular process; (F) intermediate sensory complex, 1 — stelex sensillum, 2 — medusoid sensillum.

sensillum (Fig. 2F-1) and one medusoid sensillum with short papillae (Fig. 2F-2).

The first instar is similar in general habitus (Fig. 2A) to that of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), *N. aenigma* (Goeden 2000b), and *N. appendiculata* (Goeden 2000c). However, unlike *N. viridescens,* but like *N. wilsoni, N. aenigma,* and *N. appendiculata,* the dorsal sensory organ of the first instar of *N. footei* is well defined (Figs. 2B-2, C-1, D-1), as is the anterior sensory lobe (Figs. 2B-3, C-2, D-2) and integumental petal (Figs. 2B-1, C-5, D-8). Also, the pit sensory organ (Fig. 2D-6), not seen in *N. viridescens* (Goeden and Headrick 1992) and hidden in specimens viewed of *N. signifera* (Goeden 2000a), is present in *N. footei* (Fig. 2D-6), as it is in *N. wilsoni* (Goeden and Headrick 1999), *N. aenigma* (Goeden 2000b), and *N. appendiculata* (Goeden 2000c). A fused integumental petal and stomal sense organ also was reported in first instars of *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), *N. aenigma* (Goeden 2000b), and *N. appendiculata* (Goeden 2000c), as well as *Trupanea vicina* (Wulp) (Goeden and Teerink 1999b), but these structures were separated in *N. viridescens* (Goeden and Headrick 1992).

Two stelex sensilla dorso- and ventrolaterad of each posterior spiracular plate in the first instar of *N. footei, N. aenigma* (Goeden 2000b), and *N. appendiculata* (Goeden 2000c) agreed with the four such sensilla reported to ring the caudal segment of *N. wilsoni* (Goeden and Headrick 1999), but not the 10 sensilla reported to ring the caudal segment of *N. viridescens* (Goeden and Headrick 1992). The last number is probably erroneous, as discussed by Goeden (2000b). Lastly, *N. footei* lacks the minute acanthae reported to ring basally the lateral stelex sensilla on the caudal segment in *N. wilsoni* (Goeden and Headrick 1999), where the upright acanthae among them number one to three and are pointed; in *N. aenigma* (Goeden 2000b), where the upright acanthus is solitary and rounded apically; and in *N. appendiculata* (Goeden 2000c), where the three basal acanthae are present, but poorly developed.

Second instar: White, elongate-cylindrical, rounded anteriorly, truncated posterodorsally (Fig. 3A), body segments well-defined, anterior third of meso- and metathorax and abdominal segments A-1 through A-6 circumscribed anteriorly by minute acanthae also present on abdominal pleura; dorsal sensory organ not well-defined, flattened (Figs. 3B-1, C-1, D-1); anterior sensory lobe (Figs. 3C-2, D-2) with terminal sensory organ (Figs. 3C-3, D-3), lateral sensory organ (Fig. 3D-4), supralateral sensory organ (Fig. 3D-5), and pit sensory organ (Fig. 3D-6); stomal sense organ (Figs. 3C-4, D-7) ventrolaterad of anterior sensory lobe; mouthhook bidentate (Figs. 3B-2, C-5, D-8); median oral lobe laterally compressed (Fig. 3C-6); four papilliform, integumental petals in each of two separate rows dorsad of each mouthhook (Figs. 3C-7, D-9); at least eight oral ridges, dentate along posterior margins, in vertical series laterad of oral cavity (Figs. 3B-3, C-8, D-10); prothorax, circumscribed anteriorly by at least two rows of posteriorly-directed, minute acanthae (Figs. 3B-4, C-9, D-11); anterior thoracic spiracle with three, doliform papillae (Fig. 3E); lateral spiracular complexes not seen; caudal segment with two stelex sensilla dorsolaterad and ventrolaterad of posterior spiracular plate; posterior spiracular plate bears three ovoid rimae (Fig. 3F-1), ca. 0.011 mm long, and four interspiracular processes (Fig. 3F-2), each with two to four, simple branches with one or two, apical teeth, longest branch measuring 0.009 mm; intermediate sensory complex with a stelex sensillum (Fig. 3F-3) and a medusoid sensillum (Fig. 3F-4).

The habitus of the second instar of *N. footei* (Fig. 3A) is more like that of *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), *N. aenigma* (Goeden 2000b), *N. appendiculata* (Goeden

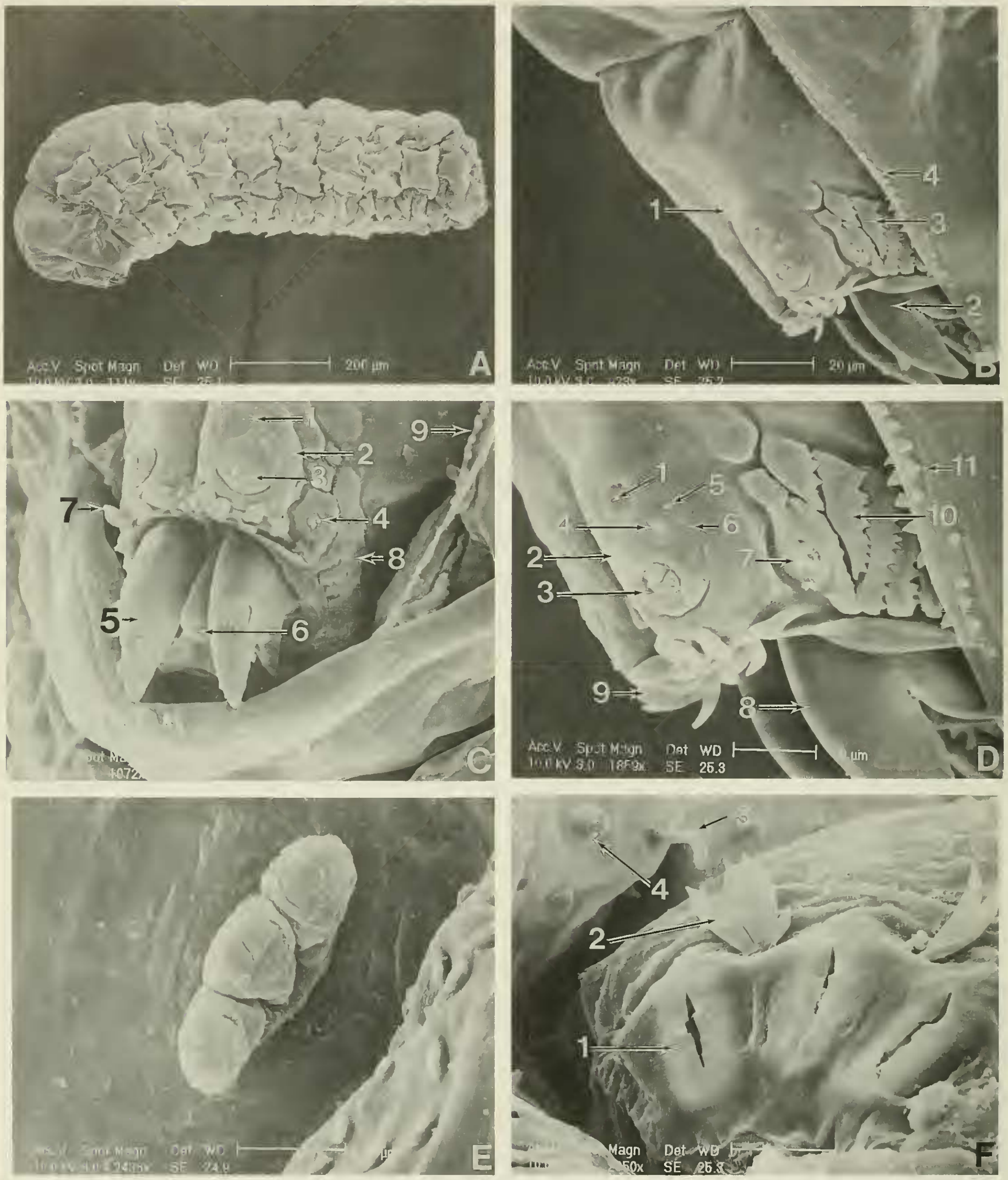

Fig. 3. Second instar of *Neaspilota footei:* (A) habitus, anterior to left; (B) gnathocephalon, lateral view, 1 — dorsal sensory organ, 2 — mouthhook, 3 — oral ridge, 4 — minute acanthae; (C) gnathocephalon, frontolateral view, 1 — dorsal sensory organ, 2 — anterior sensory lobe, 3 — terminal sensory organ, 4 — stomal sense organ, 5 — mouthhook, 6 — median oral lobe, 7 — integumental petal, 8 — oral ridge, 9 — minute acanthae, (D) lateral view of gnathocephalon, 1 — dorsal sensory organ, 2 — anterior sensory lobe, 3 — terminal sensory organ, 4 — lateral sensory organ, 5 — suprlateral sensory organ, 6 — pit sensory organ, 7 — stomal sense organ, 8 — mouthhook, 9 — integumental petal, 10 — oral ridge, 11 — minute acanthae; (E) anterior thoracic spiracle; (F) posterior spiracular plate, 1 — rima, 2 — interspiracular process, 3 — intermediate sensory complex, stelex sensillum, 4 — medusoid sensillum.

2000c), *N. pubescens* (Goeden 2000d), and *N. achilleae* (Goeden 2001) than the "barrel-shaped" (doliform) second instar of *N. viridescens* (Goeden and Headrick 1992). The dorsal sensory organ of *N. footei* is not well-defined in the second instar (Figs. 3B-1, C-1, D-1), like *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. aenigma* (Goeden 2000b), and *N. achilleae* (Goeden 2001), but unlike *N. signifera* (Goeden 2000a), *N. appendiculata* (Goeden 2000c), and *N. pubescens* (Goeden 2000d), in which this organ is well-defined. The integumental petals of the second instars of all eight species studied to date are papilliform, but are only four in number above each mouthhook in *N. achilleae* (Goeden 2001), like *N. signifera* (Goeden 2000a), but are six in number in *N. viridescens* (Goeden and Headrick 1992) and *N. pubescens* (Goeden 2000d), seven in *N. appendiculata* (Goeden 2000c) and *N. wilsoni* (Goeden and Headrick 1999), and eight in *N. aenigma* (Goeden 2000b) and *N. footei* (Figs. 3C-7, D-9). Compared to five papillae on the anterior spiracle of the second instar of in *N. pubescens* (Goeden 2000b) and eight in *N. appendiculata* (Goeden 2000c), *N. footei* only has three papillae (Fig. 3E), like the three or four papillae reported in second instars of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), *N. aenigma* (Goeden 2000b), and *N. achilleae* (Goeden 2001). Finally, the interspiracular processes of *N. footei* (Fig. 3F-2) each bear two to four branches, like those of *N. signifera* (Goeden 2000a), but not one to four branches like *N. aenigma* (Goeden 2000b) and *N. pubescens* (Goeden 2001), nor five to nine branches like *N. viridescens* (Goeden and Headrick 1992), two to six branches like *N. wilsoni* (Goeden and Headrick 1999), nor four branches like *N. appendiculata* (Goeden 2000c) and *N. achilleae* (Goeden 2001).

Third instar: Pale yellow, elongate-ellipsoidal, with posterior spiracular plate dark brown to black, tapering and truncated anteriorly; posterior spiracular plate on caudal segment flattened and upturned dorsally ca. 60° (Fig. 4A), minute acanthae circumscribe anterior fifth of mesothorax, anterior fourth of metathorax and first abdominal segment (A1), and all of remaining abdominal segments, except for pleura of segment A2, posterior half of A7, and most of A8, dorsa of abdominal segments A7 and A8 also covered with minute acanthae; gnathocephalon conical (Fig. 4B); dorsal sensory organ defined by a crescentric fold (Figs. 4C-1, D-1) attached dorsally (Figs. 4C-1, D-1) and punctured peripherally by pores (Fig. 4D-2); anterior sensory lobe (Figs. 4B-1, C-2, D-3) bears terminal sensory organ (Fig. 4D-4), lateral sensory organ (Fig. 4D-5), supralateral sensory organ (Fig. 4D-6), and pit sensory organ (Fig. 4D-7); 10 papilliform (including two small, central) or spatulate, integumental petals in two rows above each mouthhook (Figs. 4C-3, E-1); at least seven oral ridges (Fig. 4C-4), toothed ventrally and lateral to oral cavity; stomal sense organ (Figs. 4C-5, D-8) ventrolaterad of anterior sensory lobe; mouthhook (Figs. 4B-2, C-6, E-2) tridentate; median oral lobe reduced, laterally flattened, (Fig. 4E-3); gnathocephalon bears at least three verruciform sensilla posteriorad of each anterior sensory lobe and oral ridges (Figs. 4B-3, C-7); prothorax circumscribed by minute acanthae (Fig. 4B-4); verruciform sensilla circumscribe prothorax posteriorad of minute acanthae (Fig. 4B-5); anterior thoracic spiracle on posterior margin of prothorax bears three doliform papillae (Fig. 4F); mesothoracic and metathoracic lateral spiracular complexes with five and four verruciform sensilla, respectively, each complex alligned vertically, mesothoracic spiracle greatly reduced (not shown) and metathoracic spiracle not found; lateral spiracular complex of abdominal segment A-1 with a spiracle (Fig. 5A-1) and four verruciform sensilla, one dorsoposteriorad of, one posteriorad of, and two ventroposteriorad of the spiracle, the upper and first

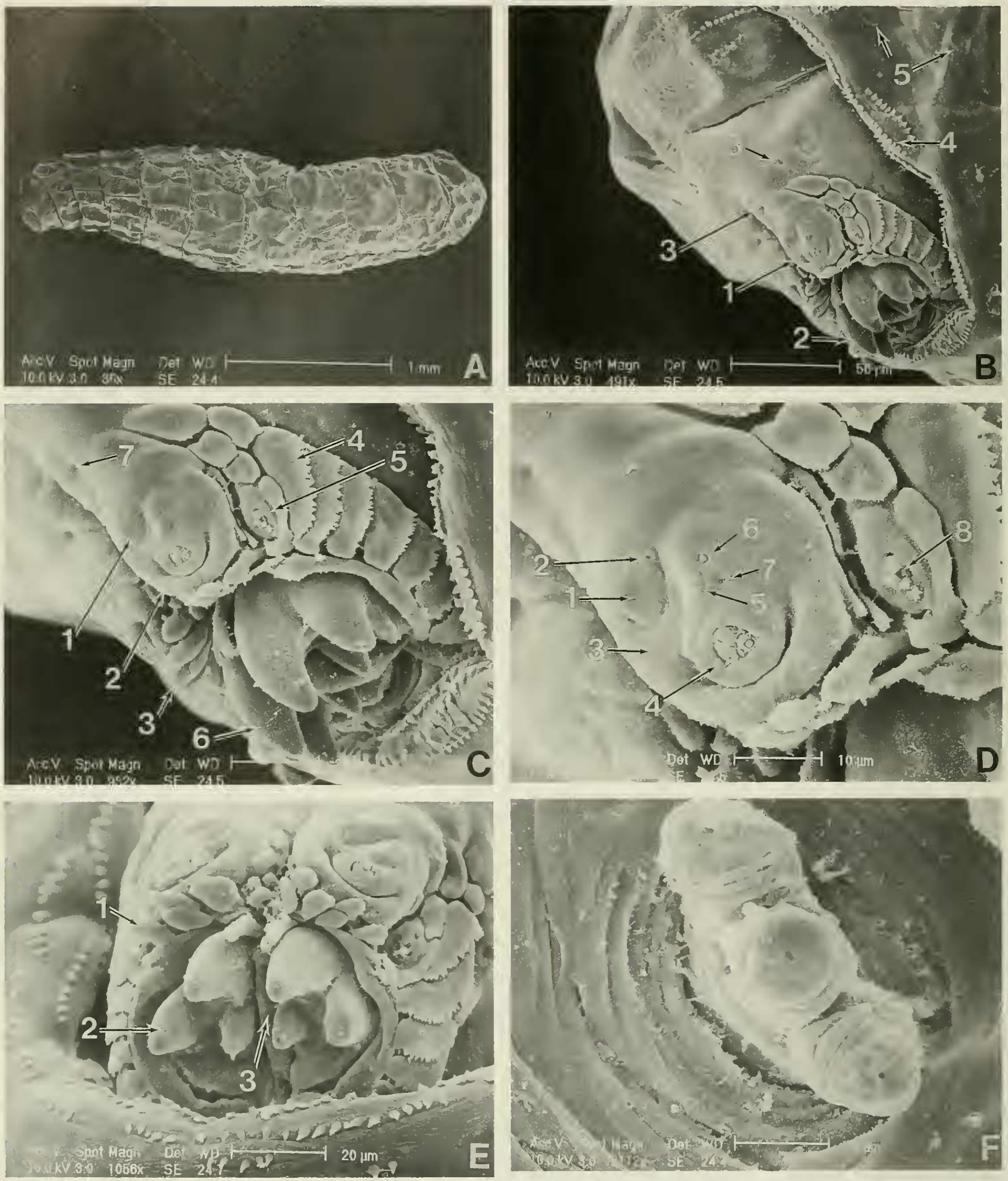

Fig. 4. Third instar of *Neaspilota footei:* (A) habitus, anterior to left; (B) gnathocephalon, frontolateral view, 1 — anterior sensory lobe, 2 — mouthhook, 3 — verruciform sensillum, 4 — minute acanthae, 5 — verruciform sensilla; (C) gnathocephalon, frontolateral view, 1 — dorsal sensory organ, 2 — anterior sensory lobe, 3 — integumental petal, 4 — oral ridge, 5 — stomal sense organ, 6 — mouthhook, 7 — verruciform sensillum; (D) anterior sensory lobe, 1 — dorsal sensory organ, 2 — peripheral pore, 3 — anterior sensory lobe, 4 — terminal sensory organ, 5 — lateral sensory organ, 6 — supralateral sensory organ, 7 — pit sensory organ, 8 — stomal sense organ; (E) oral cavity, 1 — integumental petal, 2 — mouthhook, 3 — median oral lobe; (F) anterior thoracic spiracle.

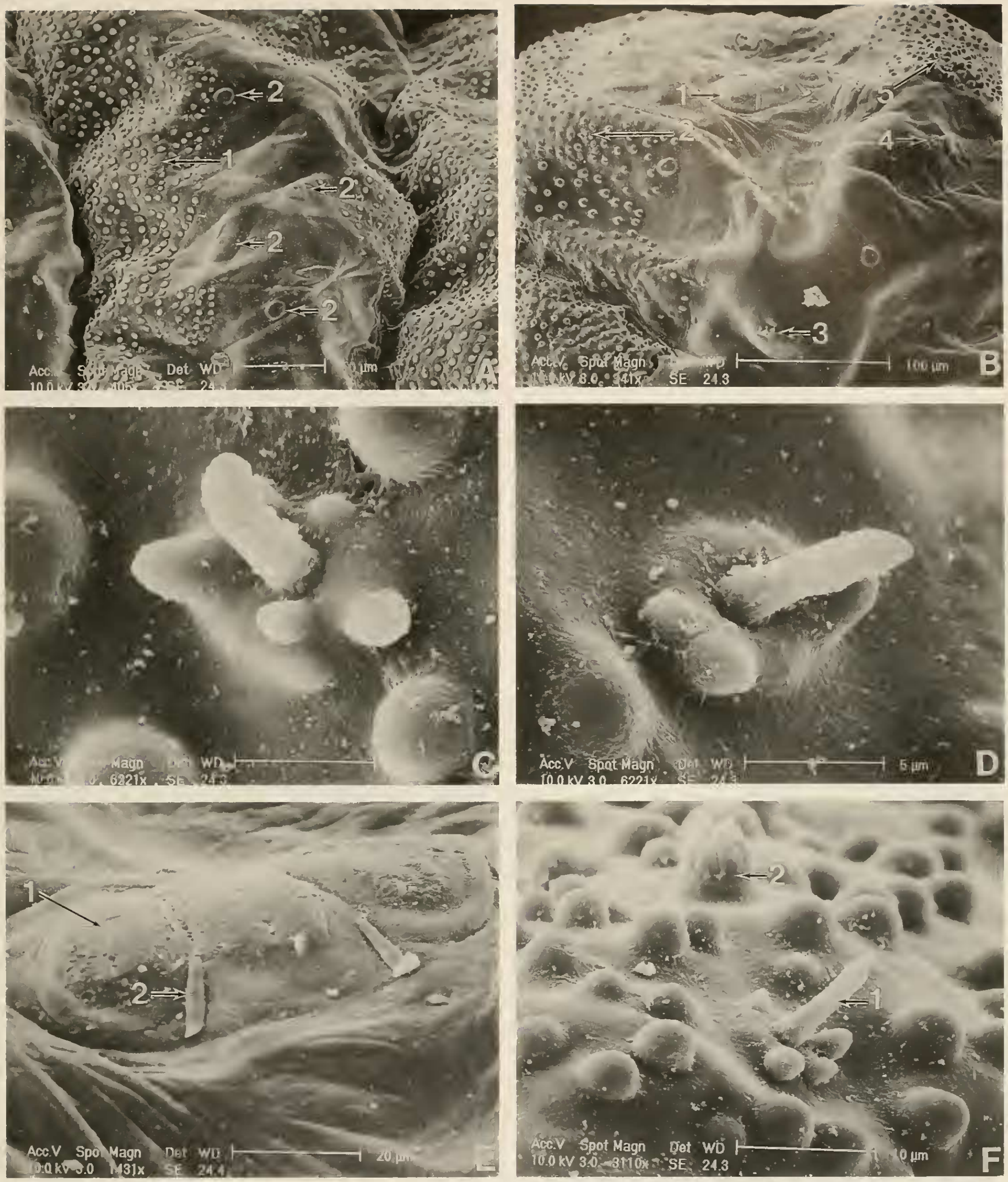

Fig. 5. Third instar of *Neaspilota footei*, continued: (A) first abdominal, lateral spiracular complex, 1 — spiracle, 2 — verruciform sensilla; (B) caudal segment, 1 — posterior spiracular plate, 2 — dorsolateral stelex sensillum, 3 — lateral stelex sensillum, 4 — ventrolateral stelex sensillum, 5 — intermediate sensory complex; (C) lateral stelex sensillum; (D) ventrolateral stelex sensillum, (E) posterior spiracular plate, 1 — rima, 2 — interspiracular process, (F) intermediate sensory complex, 1 — stelex sensillum, 2 — medusoid sensillum.

ventroposterior sensilla aligned ventrally (Fig. 5A-2), as are the other two posteriorad of the first pair (Fig. 5A-2); a stelex sensillum dorsolaterad (Fig. 5B-2), laterad (Figs. 5B-3, C), and ventrolaterad (Figs. 5B-4, D) of posterior spiracular plate, each sensillum surrounded basally by four or five, minute acanthae (Figs. 5C, D), smaller than other minute acanthae (Figs. 5C, D); each posterior spiracular plate (Fig. 5E) bears three ovoid rimae, ca. 0.014 mm in length (Fig. 5E-1), and four, simple or forked interspiracular processes, each 0.014 mm long (Fig. 5E-2); intermediate sensory complex (Fig. 5F) with a stelex sensillum (Fig. 5F-1), surrounded basally by reduced minute acanthae (Fig. 5F-1), and a medusoid sensillum (Fig. 5F-2).

The habitus of the third instar of *N. footei* is like that reported for *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), *N. aenigma* (Goeden 2000b), *N. appendiculata* (Goeden 2000c), *N. pubescens* (Goeden 2000d), and *N. achilleae* (Goeden 2001). The pattern of the minute acanthae that circumscribe the body segments is unique for *N. footei* (see description above), but closest to *N. achilleae* (Goeden 2001) in that the acanthae increase their coverage posteriorly from the anterior fifths of the thoracic segments to include nearly all of the abdominal segments, except A7 and A8 in the former species; whereas, in *N. signifera* (Goeden 2000a), *N. appendiculata* (Goeden 2000c) and *N. pubescens* (Goeden 2000d), the anterior part of each body segment is circumscribed, in *N. aenigma* the anteriors, pleura, and posteriors of each segment are circumscribed (Goeden 2000b); in *N. wilsoni,* all intersegmental areas and all abdominal segments except the pleura are circumscribed (Goeden and Headrick 1999); and in *N. viridescens,* the intersegmental areas are free of acanthae (Goeden and Headrick 1992). Like *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. pubescens* (Goeden 2000d), and *N. achilleae* (Goeden 2001), but unlike *N. signifera* (Goeden 2000a), *N. aenigma* (Goeden 2000b), and *N. appendiculata* (Goeden 2000c), the dorsal sensory organ is not well-defined and flattened, and not dome-shaped, in the third instar of *N. footei* (Figs. 4C-1, D-1).

Additional similarities involved the integumental petals in the third instars of all six congeners examined to date, all of which are arranged in a double row above each mouthhook and papilliform or spatulate (Goeden and Headrick 1992, 1999; Goeden 2000a, b, c, d, 2001). The integumental petals differ in numbers among species and generally increase in number between the last two instars. The stomal sense organ of the third instar of *N. footei* was obscured by debris in my specimens, and could thus not be compared readily with other congeners (Figs. 4C-5, D-8), but it appears at least as complex as the stomal sense organ of the second instar (Fig. 3D-4).

The third instars of all seven species of *Neaspilota* examined to date have oral ridges with dentate ventral margins characteristically arranged in vertical series ventrolaterad of the dorsal sensory organ and laterad of the oral cavity (Goeden and Headrick 1992, 1999; Goeden 2000a, b, c, d, 2001; Fig. 4C-4). Though unfortunately partly hidden and not fully counted in *N. footei* (i.e., at least seven, Fig. 4C-4) and *N. achilleae* (Goeden 2001), the oral ridges number eight in *N. pubescens* (Goeden 2000d), seven or eight in the third instar of *N. aenigma* (Goeden 2000b), seven in *N. appendiculata* (Goeden 2000c), but six in the second and third instars of the other three congeners examined to date (Goeden and Headrick 1992, 1999; Goeden 2000a). The appearance and arrangement of these oral ridges appears to be a generic character; however, Goeden (2000c, d) confirmed that the oral ridges vary in number among third instars of some *Neaspilota* species. Also, the most ventral, eighth oral ridge of *N. pubescens* is not ventrally toothed (Goeden 2000d). The third instars of *Trupanea imperfecta* (Coquillett), *T. jonesi* Curran, *T. nigricornis* (Coquillett), *T. pseudovicina* (Hering), *T. signata* Foote, and *T. wheeleri* Curran also bear serrated oral ridges (Goeden and Teerink 1997b, 1998, 1999a; Goeden et al. 1998; Knio et al. 1996; Teerink and Goeden 1999), but these oral ridges appear to be fewer in number, and are not ar-

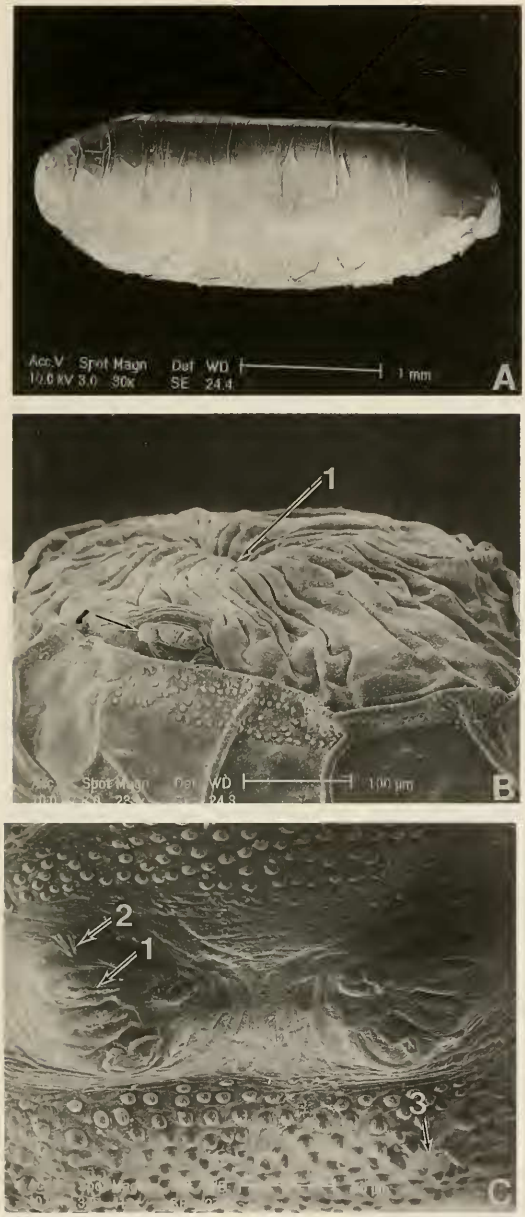

Fig. 6. Puparium of *Neaspilota footei:* (A) habitus, anterior to left; (B) anterior end, 1 — invagination scar, 2 — anterior thoracic spiracle; (C) caudal segment, 1 — rima, 2 — interspiracular process, 3 — intermediate sensory complex.

ranged in a more or less regular, vertical row laterad of the mouthhook, as in *Neaspilota*.

The mouthhooks of the third instars of *N. achilleae, N. aenigma, N. appendiculata, N. footei, N. signifera, N. viridescens,* and probably *N. pubescens,* are tridentate (Goeden and Headrick 1992, Goeden 2000a, b, c, d; Goeden 2001; Figs. 4C-6, E-2); whereas, those of the third instar of *N. wilsoni* are bidentate (Goeden and Headrick 1999). Such interspecific differences in dentation are supported by our findings that the mouthhooks of third-instar *Trupanea vicina* (Wulp) are bidentate; whereas, those of 12 other congeners examined from California are tridentate (Goeden and Teerink 1999b and citations therein).

The number and appearance of the stelex sensilla surrounding the posterior spiracular plate differ among the *Neaspilota* species examined to date. These number only four in the first instars of *N. wilsoni* (Goeden and Headrick 1999), *N. aenigma* (Goeden 2000b), and *N. appendiculata* (Goeden 2000c), but, unfortunately, were not observed with *N. signifera* (Goeden 2000a) or *N. achilleae* (Goeden 2001). This count of stelex sensilla remains at four in the second instars of *N. aenigma* (Goeden 2000b), *N. appendiculata* (Goeden 2000c), *N. pubescens* (Goeden 2000d), and *N. achilleae* (Goeden 2001), and increases to six in third instars of *N. wilsoni* (Goeden and Headrick 1999), *N. aenigma* (Goeden 2000b), *N. appendiculata* (Goeden 2000c), and *N. footei* (Figs. 5C, D). There are inter-instar (intraspecific) and interspecific differences in the incidence and appearance of the minute acanthae that may ring these stelex sensilla basally, but this was not recognized, studied or recorded by my coworkers and me until recently (Goeden 2000b, c, d, 2001). The stelex sensilla of the third instar of *N. footei* are surrounded by four or five, hemispherical, smaller-than-usual, minute acanthae (Fig. 5C, D); however, such basal minute acanthae near these stelex sensilla are lacking in the first and second instars (Fig. 2F-3).

Puparium: Mostly gray, with thoracic and posterior two or three segments blackened, ellipsoidal, and smoothly rounded at both ends (Fig. 6A); anterior end bears the invagination scar (Fig. 6B-1) and anterior thoracic spiracles (Fig. 6B-2); caudal segment circumscribed by minute acanthae; three stelex sensilla, dorsolaterad, laterad, and ventrolaterad of posterior spiracular plates; posterior spiracular plate bears three broadly elliptical rimae (Fig. 6C-1), and four, simple or forked, interspiracular processes (Fig. 6C-2); intermediate sensory complex with a medusoid sensillum and a stelex sensillum (Fig. 6C-3). Thirty-five puparia averaged 3.32 ± 0.04 (range, 2.42–3.70) mm in length; 1.13 ± 0.018 (range, 0.94–1.42) mm in width.

DISTRIBUTION AND HOSTS

Freidberg and Mathis (1986) described the known distribution of *N. footei* as forming, "... a wide, inverted U, i.e., along both coasts and across southern Canada (Canada: Ontario, Saskatchewan, United States: Alabama, California, Connecticut, Georgia, Maryland, Massachusetts, New York, North Carolina, Ohio, Oregon, Pennsylvania, Virginia)." They and Foote et al. (1993) both mapped this distribution. Freidberg and Mathis (1986, p. 52) also remarked that:

> "Although the distribution of this species, as compared to others of the genus, is suspect, we could find no significant differences between the eastern and western populations. The distributional pattern, however, could be an artifact, resulting from insufficient collecting in the Midwest and central-south United States."

The last quoted sentence probably also applies to the known distribution of *N. achilleae* in North America (Freidberg and Mathis 1986; Goeden 1989, 2001).

Freidberg and Mathis (1986) listed *Chrysothamnus* sp. and *Erigeron canadensis* L. as unconfirmed host records for single males "ex" each of these plants in Alpine Co., California, and Nassau Co., New York, respectively. Reed and Hughes (1970) and Holm et al. (1979) followed Cronquist (1943), who tranferred the latter species to *Conyza,* as *C. canadensis* (L.) Cronquist, commonly called "horseweed", a native, semi-cosmopolitan weed, common throughout the United States and southern Canada, and now found more or less worldwide (Hickman 1993). My rearing record from flower heads of *Aster occidentalis* is new (Freidberg and Mathis 1986, Goeden 1989). *Aster occidentalis* belongs to the subtribe Asterinae of the tribe Astereae, as does *C. canadensis* (Bremer 1994); however, I have never reared this or any other tephritid from seven samples of mature flower heads of the latter species, nor from three additional samples from *C. bonariensis* (L.) Cronquist (unpublished data). *Chrysothamnus* also belongs to the tribe Astereae, but to a different subtribe, the Solidagininae (Bremer 1994), and only *N. viridescens* has been reared from this genus to date (Goeden 1989, Goeden and Headrick 1992). Thus, the records for *C. canadensis* and *Chrysothamnus* both need confirmation.

BIOLOGY

Egg.—In each of 55, closed, preblossom, immature flower heads of *Aster occidentalis* an average of 1.7 ± 0.18 (range, 1–6) eggs of *N. footei* were inserted separately, pedicel-last, through the phyllaries, between them, or among the apically apressed, but separable tips of the phyllaries. Thirty-five eggs (65%) rested with their long axes parallel to the long axes of the flower heads (Fig. 7A). The remaining eggs rested at angles of 15–45°, and 45 of the 55 eggs (82%) were embedded for about half their lengths into the corollas of separate florets (Fig. 7B). An average of 1.5 ± 0.24 (range, 0–6) florets/ovules per head were damaged by oviposition, or about 2% of an average total of 62 (range, 30–85) florets/ovules/achenes counted in 53 preblossom, blossom, or postblossom flower heads. The receptacles of preblossom heads that contained eggs averaged 1.7 ± 0.06 (range, 0.85–2.56) mm in diameter.

Larva.—Upon eclosion, the 22 first instars found feeding in separate, closed, preblossom flower heads either tunneled into

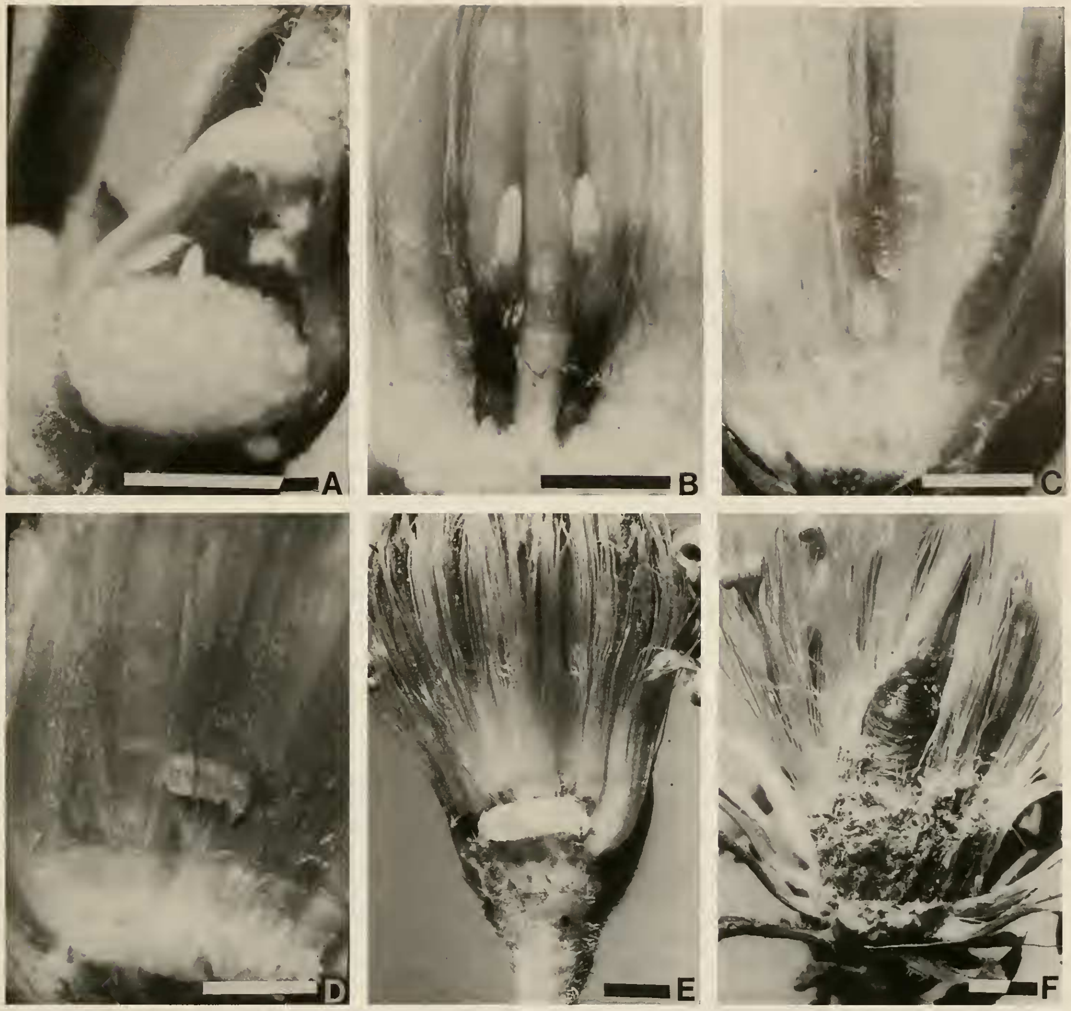

Fig. 7. Life stages of *Neaspilota footei* in *Aster occidentalis:* (A) egg between small florets in closed, preblossom flower head, (B) two eggs, partly inserted in separate corollas, (C) newly eclosed first instar, (D) second instar feeding on soft achene, (E) early third instar feeding on soft achenes, (F) overwintered puparium in dead flower head. Lines = 1 mm.

an ovule, or into a corolla before entering the ovule to which the corolla was basally attached (Fig. 7C). The receptacles averaged 2.11 ± 0.07 (range, 1.42–2.56) mm in diameter and an average of 3.9 ± 0.46 (range, 1–8) florets/ovules was damaged in these 22 flower heads. No receptacle was abraded or pitted by larval feeding. Thus, about 6% (range, 2–13%) of the average total of 62 florets/ovules/achenes in these flower heads were damaged by first instars.

Second instars continued feeding on corollas, ovules, or soft achenes in preblossom and open flower heads. They fed with their bodies parallel, angled, or perpendicular to, and their mouthparts directed towards or away from the receptacles, but always well above the receptacles (Fig. 7D). Receptacles of 26 flower heads containing second instars averaged 2.25 ± 0.07 (range, 1.75–3.13) mm in diameter. These flower heads each contained an average of 1.04 ± 0.04 (range, 1–2) larvae that had damaged an average of 8.3 ± 1.08 (range, 1–26) florets/ovules/soft achenes, or about 13% (range, 2–42%) of the average total of 62 florets/ovules/soft achenes per flower head.

Third instars (Fig. 7E) continued to feed mainly on ovules and soft achenes in preblossom, blossom, or postblossom flower heads. Fourteen flower heads that averaged 2.39 ± 0.09 (range, 1.75–2.85) mm in diameter each contained a single third instar or prepuparium. An average of 31.3 ± 2.5 (range, 11–55) of the soft achenes therein were damaged, or about 50% (range, 18–89%) of the average total of 62 ovules/soft achenes per flower head (Fig. 7E).

Third instars in flower heads fed with their long axes oriented parallel to (Fig. 7E) or at various angles to the receptacles. The receptacles were abraded or pitted in only four of a total of 69 (6%) flower heads containing third instars or overwintered puparia, thus sap apparently does not constitute a major part of the diet of *N. footei*. Goeden and Headrick (1992, 1999) and Goeden (2000c, d) described and discussed sap feeding by *N. viridescens, N. wilsoni, N. appendiculata,* and *N. pubescens,* respectively. Upon completing feeding, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and formed puparia, which constitute the overwintering stage (Headrick and Goeden 1998).

Pupa.—The receptacles of 55 overwintered flower heads that contained a single puparium (Fig. 7F) each averaged 3.5 ± 0.06 (range, 2.56–4.27) mm in diameter. *Neaspilota appendiculata* (Goeden 2000c), *N. viridescens* (Goeden and Headrick 1992), and *N. wilsoni* (Goeden and Headrick 1999) overwinter in dead flower heads as prepuparia in protective cells formed of ovule, achene, chaff, pappus, and corolla fragments cemented together by liquid feces and sap that hardened when dry. However, *N. footei* puparia are partly surrounded and protected only by uneaten achenes and fragments tightly glued to the puparia within each flower head (Fig. 7F). The adults emerge from these puparia in early spring (April).

Adult.—Adults are probably long-lived in nature, but few were reared from overwintered puparia, as many contained parasitoids or were collected after the adults already had emerged. Under insectary conditions, a single unmated male lived 104 days, and three virgin females averaged 80 ± 15 (range, 52–104) days. Such lengthy longevities compare favorably with average adult longevities reported for adults of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), *N. aenigma* (Goeden 2000b), *N. appendiculata* (Goeden 2000c), *N. pubescens* (Goeden 2000d), and *N. achilleae* (Goeden 2001).

The premating and mating behaviors of *N. footei* were not studied in the field, but were observed in one petri dish arena of the type found to be so useful with many other nonfrugivorous, tephritid species (Headrick and Goeden 1994). Premating behaviors observed with this pair of *N. footei* were abdominal pleural distension by males and side-stepping and swaying by both sexes while tracking their opposite sexes (Headrick and Goeden 1994), and rapid wing hamation by both sexes (Headrick and Goeden 1994). No trophallaxis or nuptial gift presentation was noted as reported with *N. viridescens* (Goeden and Headrick 1992). A single mating of more than 3-h duration was observed, which began during late afternoon at dusk, but was not viewed from beginning to end. This compared with average durations of 153 min reported for *N. achilleae* (Goeden 2001), 190 min reported for *N. aenigma* (Goeden 1999b), 235 min reported for *N. wilsoni* (Goeden and Headrick 1999), 238 min reported for *N. signifera* (Goeden 2000a), 285 min reported for *N. appendiculata* (Goeden 2000c), 318 min reported for *N. viridescens* (Goeden and Headrick 1992), and 1032 min reported for *N. pubescens* (Goeden 2000d). The copulatory position was as described in detail for *N. achilleae* (Goeden 2001).

Seasonal history.—The life cycle of *N. footei* in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the puparium is the principal overwintering stage. Come spring (April), adults emerge and aggregate on preblossom shoots of *A. occidentalis* to mate and subsequently oviposit in the small, newly-formed, closed, preblossom flower heads begining in late May. The larvae feed until fully grown, then pupariate in flower heads and overwinter. *Neaspilota footei* is the only species among eight species studied by us known to overwinter as puparia in southern California. *Neaspilota signifera* (Goeden 2000a), *N. aenigma* (Goeden 2000b), and *N. achilleae* (Goeden 2001) principally overwinter as adults; whereas, *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. appendiculata* (Goeden 2000c), and *N. pubescens* (Goeden 2000d) also overwinter principally in dead flower heads, but as prepuparia.

Natural enemies.—Many individual *Pteromalus* sp. (Hymenoptera: Pteromalidae) were reared from puparia of *N. footei* as solitary, larval-pupal endoparasitoids. A male and female each of *Eurytoma* sp. (Hymenoptera: Eurytomidae) and *Mesopolobus* sp. (Hymenoptera: Pteromalidae) were reared from mature flower heads of *Aster occidentalis* as probable solitary, larval-pupal endoparasitoids.

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LITERATURE CITED

Bremer, K. 1994. Asteraceae Cladistics & Classification. Timber Press, Inc., Portland, Oregon.

Cronquist, A. 1943. The separation of *Erigeron* from *Conyza*. Bull. of the Torrey Botanical Club 70: 629–632.

Foote, R. H., F. L. Blanc, and A. L. Norrbom. 1993. Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico. Cornell University Press, Ithaca, New York.

Freidberg, A. and W. N. Mathis. 1986. Studies of Terelliinae (Diptera: Tephritidae): A revision of the genus *Neaspilota* Osten Sacken. Smithsonian Contributions to Zoology 439: 1–75.

Goeden, R. D. 1987. Life history of *Trupanea conjuncta* (Adams) on *Trixis californica* Kellogg in southern California (Diptera: Tephritidae). The Pan-Pacific Entomologist 63: 284–291.

———. 1989. Host plants of *Neaspilota* in California (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 91: 164–168.

———. 2000a. Life history and description of immature stages of *Neaspilota signifera* (Coquillett) (Diptera: Tephritidae) on *Hemizonia pungens* (Hooker and Arnott) Torrey and A. Gray (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 102: 69–81.

———. 2000b. Life history and description of immature stages of *Neaspilota aenigma* Freidberg and Mathis (Diptera: Tephritidae) on *Erigeron divergens* Torrey and Gray (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 102: 384–397.

———. 2000c. Life history and description of immature stages of *Neaspilota appendiculata* Freidberg and Mathis (Diptera: Tephritidae) on *Machaeranthera canescens* (Pursh) A. Gray (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 102: 519–532.

———. 2000d. Life history and description of immature stages of *Neaspilota pubescens* Freidberg and Mathis (Diptera: Tephritidae) on *Lessingia filaginifolia* (Hooker and Arnott) M. A. Lane (Asteraceae). Proceedings of the Entomological Society of Washington 102: 878–891.

———. 2001. Life history and description on immature stages of *Neaspilota achilleae* Johnson (Diptera: Tephritidae) on *Stephanomeria* spp. (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 103:60–73.

Goeden, R. D. and D. H. Headrick. 1992. Life history and descriptions of immature stages of *Neaspilota viridescens* Quisenberry (Diptera: Tephritidae) on native Asteraceae in southern California. Proceedings of the Entomological Society of Washington 94: 59–77.

———. 1999. Life history and description of immature stages of *Neaspilota wilsoni* Blanc and Foote (Diptera: Tephritidae) on *Hazardia squarrosa* (Hooker and Arnott) E. Greene (Asteraceae). Proceedings of the Entomological Society of Washington 101: 897–909.

Goeden, R. D. and J. A. Teerink 1997a. Life history and description of immature stages of *Xenochaeta dichromata* Snow (Diptera: Tephritidae) on *Hieracium albiflorum* Hooker in central and southern California. Proceedings of the Entomological Society of Washington 99: 597–607.

———. 1997b. Life history and description of immature stages of *Trupanea signata* Foote (Diptera: Tephritidae) on *Gnaphalium luteo-album* L. in southern California. Proceedings of the Entomological Society of Washington 99: 748–755.

———. 1998. Life history and description of immature stages of *Trupanea pseudovicinia* Hering (Diptera: Tephritidae) on *Porophyllum gracile* Bentham (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 100: 361–372.

———. 1999a. Life history and description of immature stages of *Trupanea wheeleri* Curran (Diptera: Tephritidae) on Asteraceae in southern California. Proceedings of the Entomological Society of Washington 101: 414–427.

———. 1999b. Life history and description of immature stages of *Trupanea vicina* (Wulp) (Diptera: Tephritidae) on wild and cultivated Asteraceae in southern California. Proceedings of the Entomological Society of Washington 101: 742–755.

Goeden, R. D., J. A. Teerink, and D. H. Headrick. 1998. Life history and description of immature stages of *Trupanea jonesi* Curran (Diptera: Tephritidae) on native Asteraceae in southern California. Proceedings of the Entomological Society of Washington 100: 126–140.

Headrick, D. H. and R. D. Goeden. 1994. Reproductive behavior of California fruit flies and the classification and evolution of Tephritidae (Diptera) mating systems. Studia Dipterologica 1(2): 194–252.

———. 1998. The biology of nonfrugivous tephritid fruit flies. Annual Review of Entomology 43: 217–241.

Hickman, J. C. (ed.) 1993. The Jepson Manual. University of California Press, Berkeley and Los Angeles.

Holm, L., J. V. Pancho, J. P. Herberger, and D. L. Plucknett. 1979. A Geographical Atlas of World Weeds. John Wiley and Sons, New York, Chichester, Brisbane, Toronto. 391 pp.

Knio, K. M., R. D. Goeden, and D. H. Headrick. 1996. Descriptions of immature stages of *Trupanea nigricornis* and *T. bisetosa* (Diptera: Tephritidae) from southern California. Annals of the Entomological Society of America 89: 1–11.

Reed, C. F., and R. O. Hughes. 1970. Selected weeds of the United States. U.S. Department of Agriculture, Agricultural Research Service, Agriculture Handbook No. 366. 463 pp.

Teerink, J. A. and R. D. Goeden. 1999. Description of the immature stages of *Trupanea imperfecta* (Coquillett). Proceedings of the Entomological Society of Washington 101: 75–85.